ON VOLTZIOPSIS, A SOUTHERN CONIFER OF LOWER TRIASSIC AGE

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(With seven text figures and one plate.)

ABSTRACT

Shoots ascribed to *Voltziopsis africana* Seward are described, with cuticular detail. These compare very closely with the shoot system, with an attached seed cone, called *V. wolganensis* sp. nov., which is associated with pollen of the *Strotersporites* Wilson sort. The shoot called *Brachyphyllum angustum* Walkom is redescribed though Walkom's specimens cannot be found, and proves to be so close to the species referred to *Voltziopsis* that it is reclassified *V. angusta* (Walkom) comb. nov. The material considered comes from the Lower Triassic of New South Wales, and reasons are given for considering all *Voltziopsis* specimens Lower Triassic also. The classification of *Voltziopsis* in the Coniferales is discussed.

INTRODUCTION

The genus *Voltziopsis* Potonié has been known for a long time, but only from poor material, and has remained, despite Florin's (1944) description, a rather vague entity. In the Geological and Mining Museum, Sydney, there is a remarkable specimen showing a seed cone attached to a large spray of foliage. The cone agrees with *Voltziopsis*, so the foliage is referred to *Voltziopsis* also. With this information, the shoots of the type species, *V. africana* Seward can be re-described with cuticular detail, and another shoot placed in the genus. So redefined *Voltziopsis* proves to be a small genus, probably only Lower Triassic, comparing in a very interesting way with the taxodiaceous genera, *Cryptomeria* Don and *Athrotaxis* Don, and with the isolated cone unit *Swedenborgia* Nathorst. It seems unlikely that *Voltziopsis* is derived from the southern Permian conifers.

DESCRIPTIONS

Family VOLTZIACEAE

Genus **VOLTZIOPSIS** Potonié

Type species: *Voltziopsis africana* Seward

1899 *Voltziopsis* Potonié, pp. 303-304, fig. 304.

1900 *Voltziopsis* Potonié, pp. 503-504, fig. 29, a-g.

1934 *Voltziopsis* Potonié (*V. africana* Seward), Seward, pp. 387-388, pl. 19, figs. 4, 5; pl. 20, figs. 9, 10.

1944 *Voltziopsis* Potonié: Florin, pp. 486-488, pl. 181-182, figs. 3-5, text fig. 53.

(Further references are given under the species.)

Diagnosis (*emended*). Conifers showing irregularly and sparingly branched shoots. Leaves dimorphic even on same shoot; smallest scale-like, about 3 mm. long and 2 mm. wide, more or less triangular, apex rounded or acute, about half as thick as broad. Largest leaves 2 or 3 cms. long and 3 to 5 mms. wide, directed forward, or forwards and outwards, and if the latter, showing tendency to be twisted into two rows up the shoot. Long leaves 2 or 3 mms. thick at base. All leaves having a thin but not scarious margin, lower (abaxial) surface rounded or angled, but lacking a distinct keel, upper surface usually concave, or flat, rarely slightly raised over the midrib. All variants between extremes of leaf form found.

Cuticle thin, 0.5-1.5μ (all measurements from folds) of different thickness on two leaf surfaces. Leaf unequally amphistomatic, with most stomata on the upper surface: all epidermal cells set more or less in rows and stomata also usually in obscure rows, orientation longitudinal or various. Lower leaf surface showing equidimensional or elongated epidermal cells, and a few stomata mainly towards leaf base. On upper leaf surface cells at margin as those on leaf under surface, towards "midrib" cells set less regularly, and cuticle thinner. Most stomata borne towards the midline of the leaf, but (probably) a non-stomatiferous "midrib" present. Cuticle surface smooth, cell outlines not thick (about 4μ or less), straight and unpierced by holes. Stomata chiefly mono-cyclic, rarely dicyclic with one to six encirling cells. Stomata showing four to about eight subsidiary cells, having a smooth dorsal surface and not produced over the stomatal pit. Subsidiary cells disposed with two lateral and two terminal members or in a ring of four to six equal cells. Encircling cells, where present, unspecialised except by position. Guard cells only slightly sunken in a more or less rectangular pit, feebly cutinised. No cutinised hypodermis present. Venation unknown.

Pollen cone unknown.

Seed cone terminal on a short branch just like a normal vegetative branch, cone cylindrical about 2.5 cms. long and 1.5 cms. wide, consisting of (estimated) 25 units closely packed together. Unit consisting of bract and cone scale (= seed scale complex or flower of Florin). Bracts forked, narrow, as long as or longer than the cone scale. Cone scale consisting of a thick but flattened stalk expanding apically into five (rarely six) lobes, not inserted quite at the same level. Each lobe bearing a single inverted seed, free from the lobe, but

FIG. 1.—*Voltziopsis africana*, *A*; *V. angusta*, B-D. A: A long shoot, lower right. To top left, the other common conifer from the Bulli roof shales. x 1. F 22426. B: Specimen showing a long leaved and a short leaved shoot, arrow marks branching (Fig. 2F). x 1.5. F 13022. C: A rather narrow shoot, with long narrow leaves. F 13021. D: Impression of a shoot with leaves of medium length. F 13022. Both x 7.

lobe showing seed stalk adnate to it. Lobes obtuse or pointed. Total length of cone scale about 8 mms. Seed (or ovule) egg shaped, with micropyle at narrower end, about 1.5 mm. long and 1.0 mm. wide. Cone probably disarticulating when ripe (or when with unfertilised seeds).

Stalk of cone scale cutinised, showing thick (3μ) cuticle over its abaxial surface, thinner cuticle over (supposed) adnate seed stalk, this surface without stomata. Lobes of cone scale showing cuticle of different thickness on two sides, showing cells more or less rectangular or trapezoid, set in somewhat irregular rows, especially irregular on thinner (presumably upper, or adaxial) surface. Stomata as on leaf; present (?) only on upper lobe surface. Bract with similar cuticles to lobe of cone scale, but unequally amphistomatic. Details of seed unknown.

Discussion. (1) *Description. Voltziopsis* was first suggested by Potonié (1899, pp. 303-304, fig. 304) to include isolated cone units and shoots from East Africa, and also a variety of other fossils, such as *Leptostrobus* Heer, now known to be different. He did not formally diagnose his genus, nor declare a type species. This latter was done by Seward (1934), as *V. africana* Seward. Florin (1944, pp. 486-488) re-described Potonié's material (including some of a later collection), and definitely excluded from the genus all but the five or six lobed seed scale complexes subtended by a forking bract. Since a cone is now found in connection with foliage, *Voltziopsis* returns to Potoniés original concept of it, only without *Leptostrobus* &c.

The genus now comprises (1) *V. africana;* the type species consisting of shoots with cuticle, and isolated non cutinised cone units (not seen by me): (2) *V. wolganensis;* consisting of a single specimen, cutinised, showing attached shoot and seed cone and associated pollen: *V. angusta,* cutinised shoots. As will be seen, the evidence for ascribing shoots to cones is circumstantial, in the case of *V. africana,* and the evidence is discussed under the species.

The branching pattern is best seen in F6620 (Pl. 1E), but other figures (Walkom 1925, pl. 30, fig. 5; Seward 1934, pl. 19, fig. 5) provide further evidence. Plainly there is no trace of a long shoot/short shoot system seen in certain species of *Voltzia* Brongniart (e.g. Schimper and Mougeot 1844 pls. 6 and 7), or in *Metasequoia* Miki among living conifers.

The dimorphism of the leaves has been noted by all authors though it is most extreme in *V. wolganensis* (Pl. 1B). However, this leaf dimorphism is somewhate different from what is seen in, e.g. *Dacrydium bidwillii* Hook f., for in both long and short leaves the leaf shape is the same (or closely similar); the variation is in size rather than form. the gross form of the leaf is the same in all three species treated here; the lower surface is seen to be somewhat raised, and where a leaf lies apart from the rest (Figs. 1C; 2B, D) this appearance, on Walton's compression theory, arises because the upper surface was concave, and the matrix has formed a mould upon which the leaf has collapsed. Seen compressed laterally, the leaf is thick, but there is no sign of a keel (Figs. 2B, C, F), presumably therefore, the leaf lower surface was rounded-convex. In some specimens (Fig. 2D) the leaf margin is seen to be thin, and this is confirmed from cuticle preparations which sometimes show (Fig. 4D) compression folds a little way in from the margin, though in *V. africana* the leaf may be nearly flat (Fig. 5A). However, the cells at the margin are not identical on both cuticle surfaces, so the margin was not scarious. A similar appearance can be seen in the living *Araucaria excelsa* Lamb, in which the thick leaf thins abruptly to a thin but not scarious margin. The leaves may therefore be visualised as being rather like the leaves of *Athrotaxis selaginoides* Hook, in which, in fresh material, the under surface is not keeled, though the leaf is thick and the upper is flat or slightly concave or rarely ridged. In this conifer, the leaf is also unequally amphistomatic to epistomatic, but all the stomata on the upper leaf surface form a dense mass, and no " midrib " is present (Florin 1931).

The cuticle proved troublesome to prepare. The cuticle is thin, and the material apt to break up into cubes about 2 x 2 mm. or less. This means that stomatal distribution has to be deduced rather than observed. A difference in cutin thickness can be made out. By analogy with very many living conifers with more or less appressed small leaves, the thinner cuticle is supposed to be from the upper (adaxial) leaf surface, and the thicker one from the lower (abaxial) surface. The thicker cuticle (lower), shows rectangular or irregularly elongated or equidimensional cells (Figs. 4D, E) and few or no stomata. In *V. africana,* which has a cuticle easier to prepare than the others, most stomata on the lower leaf surface are found near the base of the leaf. The thinner (upper) cuticle is similar at the leaf margin (Figs. 5A; 6A) but shows stomata towards the middle of the leaf. Granted that the cuticles are correctly ascribed to their leaf surface, it is clear that most of the stomata are on the upper leaf surface. In *V. africana* and *V. wolganensis* there are some stomata on the lower leaf surface, though they are few (Fig. 4E; Pl. 1D). For *V. angusta* I was unable to find any stomata on the thicker cuticle, and here the leaf may be completely epistomatic. The cuticles are remarkably unadorned, in all species papillae (over stomata or not), simuosities in the cell outline or holes being quite absent.

The cone details are based mainly upon the single specimen F6620, shown in Pl. 1C which being much better preserved sheds light on the cone units of *V. africana.* No difference can be detected between the branch bearing the cone and any others, both bearing leaves of the same sort. The number of cone units seen on two sides is 12 or 13, and I suppose an equal number lay on the other surface. The whole forms a dense cone-like structure, each unit overlapping half to three quarters of the one above. The arrangement of units is spiral. The form of each unit is uniform, but the sizes of the parts varies considerably (a matter discussed below). The bract is forked about two thirds the way along its length (Florin 1944, pl. 181, fig. 3, text-fig. 53 and Figs. 3A, C) and cuticle preparations from it show that it is amphistomatic. The stalk to the cone scale (= seed scale complex of Florin) is thick but still wider (Fig. 3F), so that it was flattened. The cuticle of a

FIG. 2.—*Voltziopsis africana* A, B, D, E; *V. wolganensis*, C; *V. angusta* F. A, B, Apices of two shoots, with rather long narrow leaves. F 22426 and 534. C, D, F: Parts of shoots with leaves, upper surface slightly raised (C), concave, and leaves twisted into two rows (D) F 2260, F 22426, F 13022. All x 7. E: A length of shoot with untwisted leaves x 1.5. 2938.

lobe is shown in Fig. 5D. The cuticle of the lobe shows a strip of thinner cuticle with narrower cells at one edge. The strip coresponds in position to a low ridge running from the seed to the cone scale stalk, interpreted by Florin (*loc. cit.*) and I as a seed stalk, which, since its cuticle is continuous with that of the rest of the lobe, was adnate to the lobe (cf. Tison 1909 on *Saxegotha conspicua* (Lindl.)). The five lobes do not all fit onto the stalk at quite the same level (Fig. 3F), a situation slightly recalling *Pseudovoltzia* Florin. Compressed laterally the lobes were thick (Fig. 3F) possibly triangular in section, and probably the whole unit lapped round the cone axis, for parts of some lobes are folded (Fig. 3A). The cuticle of the lobes is shown in Figs. 4B, D), and like the leaves shows cuticles of different thicknesses with a few stomata seen only on the thinner. As for the leaves it is supposed that the stomata were borne (or chiefly borne) on the upper surface of the lobe, though the preparations are so small that there could very well be a few stomata, as on the lower surface of the leaf, that have been missed.

A point of considerable interest is that the cuticle, including stomata, of both leaf and cone scale, is identical, though the stomata on the cone scale are of the simpler sort seen on the leaf. This provides another fragment of evidence that one may properly associate organs on the strength of their similar cuticle.

The material described by Florin (1944) was not well preserved, and with some doubt, the seeds were reconstructed as upright, (text-fig. 53). However, in *V. wolganensis* it is now almost certain that they are inverted, though without cuticle preparation to demonstrate the micropyle, the matter is not quite settled. At the distal (chalazal) end the seed passes smoothly into the fused seed stalk, but at the other end, the seed is separate from the lobe, and of extremely thin material, like the micropyle of e.g. *Umkomasia* Thomas where one can demonstrate the various layers expected at the micropyle (see Harris 1964, pl. 2 for example). Despite several efforts, I was not able to get a cuticle preparation from a seed that could be interpreted. Only wisps of excruciatingly thin cuticle remained.

From the comparative abundance of isolated cone units, it may be that the *Voltziopsis* cone disarticulated when ripe, or perhaps if the ovules were not pollinated, as happens in some species of *Araucaria*.

(2) *The age of Voltziopsis. Voltziopsis* has always been supposed to be Triassic. Seward (1934) with hesitation dated his material of *V. africana* from East Africa as Upper Triassic, and this is accepted by Florin (*loc. cit.*), Carpentier (1935) placed his material, also hesitatingly, in the Lower Triassic. I suggest that *Voltziopsis* is only Lower Triassic. There are several points. (*a*) *Voltzia* cf. *liebeana* of duToit (1927) from the Molteno, once thought to be *Voltziopsis* (Florin 1940) is now placed with *Rissikia*, a very different conifer. (*b*) The grounds on which Seward (1934) was inclined to place his flora in the Upper Triassic were essentially the presence of *Baiera*-like and *Desmiophyllum*-like leaves. In the Gondwana Triassic these are two very poorly known complexes that probably range the Triassic, and Jurassic too. The evidence they provide is unconvincing. On the other hand the Tanga flora contains no undoubted corystosperms, in particular none of the exceedingly common (indeed dominant) species such as *Dicroidium odontopteroides* (Morris) Gothan) mainly an Upper Triassic species. This negative evidence does not of itself invalidate Seward's conclusions, but it does make his flora a rather remarkable one, if Upper Triassic. (*c*) Carpentier's flora containing *Voltziopsis* contains various other conifers, the leaf *Thinnfeldia callipteroides, Lepidopteris madagascarienses,* but again, no definite corystosperms, unless the single pinna tentatively ascribed to *Supaia* White (pl. 2, fig. 5) is a *Dicroidium* pinna. This flora comes from the same series of rocks that have since been dated on their vertebrates as Lower Triassic (Lehman 1952, pp. 190-196; 1961, pp. 151-152). (*d*) In New South Wales the foliage ascribed to *V. africana* comes only, as far as I can discover, from the roof shales of the Bulli Seam in Hennelly's (1958) Transition Zone; a horizon no younger than Lower Triassic age, and also incidentally with *Ginkgo*- and *Baiera*-like leaves,and possibly basal Triassic (see Balme 1963). It is not known for certain where the specimen of *V. wolganensis* comes from, but the best guess (below p. 14) is that it comes from a horizon close to the top of the Permian. The shoot *Voltziopsis angusta* comes from the Gosford Formation, at the top of the Narrabeen Group; also of Lower Triassic age. Taken together these arguments render a Lower Triassic age for *Voltziopsis* more likely than any younger age.

(3) *Generic Comparison.* The cone units of *Voltziopsis* are unlikely to be confused with anything else; the various genera at one time grouped with it are now known to be quite different (Florin 1944). The dimorphic foliage is also unusual, as is to a less extent the leaf shape and stomatal distribution as they are interpreted. Dimorphic foliage, of rather a different sort and based on a system of long shoots and foliage spurs, is seen in some *Voltzia* species (Schimper and Mougeot 1844, Schimper 1869, Brongniart 1828), but the cuticles of these shoots are unknown, Kräusel (1943) figures a cuticle as ?*Voltzia*; it is quite different from *Voltziopsis*. *Swedenborgia* Nathorst (Harris 1935, Florin 1944) has a structure basically like that of *Voltziopsis*, but with a small, simple bract adnate over most of its length to the cone scale. *Rissikia* (see first of these notes) is slightly similar in its cuticle, but has bilaterally flattened leaves, and usually, lappetts or papillae over the stomata. *Walkomia* Frenguelli *non* Florin is discussed below. Among Permian conifers *Walkomiella* and *Buriadia* Seward and Sahni (see Florin 1944) are very different in leaf shape and (*Walkomiella*) cuticle and cone scale. *Paranocladus* Florin (1944) could be compared in its stomatal arrangements, but differs in its branching pattern, leaves, and in being more or less equally amphistomatic. *Voltziopsis* thus shows little if any approach to the southern Permian conifers.

Voltziopsis africana Seward

Pl. 1, A, D. Figs. 1A; 2A, B, D, E; 3B, D; 4A; 5A-C; 7D.

1899 *Voltziopsis* Potonié, pp. 303-304, fig. 304. Shoot and cone unit, latter taken as holotype. E. Africa.

FIG. 3.—*Voltziopsis africana*, B, D; *V. wolganensis*, A, C, E, F; pollen associated with *V. wolganensis*, G. A: Part of a cone unit seen from the abaxial side, showing part of the bract. C: An isolated unit, seen from adaxial side, the leftermost lobe outlined from the counterpart of this specimen. E: Part of a cone unit showing pointed lobes of the cone scale. F: A cone unit attached to the cone axis, seen adaxial view (note, lobes not all inserted at quite the same level). All x 7. F 2260. B, D; fragments of cuticle with a stoma, probably from leaf lower surface, x 200 and x 400. F 22426. G, A grain in rotated proximal polar view. x 600. F 2260.

1900 *Voltziopsis* Potonié: Potonie, pp. 503-504, fig. 29, a-g. Material as above.

?1922 *Voltzia* sp. Seward, pl. 17, figs. 8 and 9 only. Very fragmentary material, Tanganyika.

?1927 *Voltzia* sp. Gothan, p. 151, pl. 19, fig. 13 a, b. Obscure cone units.

1934 *Voltziopsis africana* Seward, p. 388, pl. 19, fig. 4 (cone unit), pl. 19, fig. 5 and pl. 20, fig. 9 (shoots). Tanganyika, ? from several localities.

1935 *Voltzia heterophylla* Carpentier non Brongniart, pl. 4, fig. 7 (shoot), pl. 5, figs. 8, 10, 11 (cone units), ? pl. 1, fig. 6 (shoot).

?1935 *Brachyphyllum* sp. Carpentier, pl. 1, fig. 3.

1936 *Voltzia heterophylla* Carpentier non Brongniart, pl. 5, figs. 9, 10. Carpentier's material from Madagascar. Excluded are 1935 pl. 1, figs. 4, 5, 7; pl. 2, figs. 12, 13; pl. 5, figs. 9, 12, 13.

1940 *Voltziopsis africana* Seward: Florin, pp. 57-58. Discussion.

1944 *Voltziopsis africana* Seward: Florin, pp. 486-488, pl. 181-182, figs. 3-5, text-fig. 53. Redescription of Potonié's material, with extended discussion.

Holotype: Potonié, (1899) fig. 304 (cone scale).

Locus typicus: In the vicinity of Tanga, E. Africa; Triassic, probably Lower Triassic.

Diagnosis (emended). Shoots sparingly branched, leaves only slightly dimorphic, wide, nearly flat, generally with obtuse apex, varying from 3 mm. long and 3 mm. wide and very obtusely pointed, to 7 mm. long and 2-4 mm. wide, bluntly pointed. Leaves generally borne all round shoot, but sometimes standing out at up to 90° from axis, and rarely slightly twisted to lie in two rows.

Shoot cuticle thin but tough, 1.5μ and 1μ, showing cells on both surfaces of rectangular to somewhat irregular shape, and often cell rows very obscure or absent. Cells about 54μ in length and 34μ wide, of wall thickness 6μ. Stomata few and scattered on thicker (lower) leaf surface, and usually with four subsidiary cells, two lateral and two terminal, and no encircling cells. On thinner (upper) leaf surface stomata scattered, or in obscure rows, with one to five epidermal cells between subsidiary cells of adjacent stomata, or in groups of 3-5 having subsidiary cells touching. Stomata monocyclic or, less often, irregularly dicyclic, subsidiary cells (on upper leaf surface) tending to form ring of 4-6 more or less wedge shaped cells of equal size.

Seed cone units 10-17 mm. long and 10-14 mm. wide; bract about 19 mm. long, forked in its last third, contracting to 1 mm. broad below; cone scale consisting of five (rarely six) lobes, cone scale 2-4 mm. wide below, lobes rounded at apex, 4-6 mm. from apex to point of union with other lobes, and about 3 mm. wide at maximum. Seed probably inverted, (?) about half as long as free lobes. (paraphrased from Florin 1944, pp. 486-487, but seeds now described as probably inverted not upright).

Description and discussion. Voltziopsis africana is a rather uncommon component of the Bulli roof shales flora. I have found it sparingly at Nattai Bulli, Oakdale and as fragments at South Bulli, Bulli and South Clifton. In the Mitchell collection in the Australian Museum there is another specimen, F22426, localised by Mitchell as coming from Wonoona Park [*sic.*]. This locality is almost certainly wrong, for this place, now Richardson Park, Woonona, lies on stabilised dune, at the level of the extreme base of the Coal Measures. Further, the associate is another conifer known only from the Bulli roof shales. Of course, Mitchell may have found the specimen in the fill, when the park was laid out.

No branching specimen has been seen, but it would seem from F22426 that branching is sparse. Indeed, it is possible that this piece did branch where it takes a sharp bend to the right, but there is no clear evidence that it did. In this species, as in the others, the impression of the upper leaf surface, around which the leaf is supposed to have collapsed, is convex; thus the leaf surface was concave (Fig. 2D), though in many cases the leaf is very nearly, or entirely, flat. As in the other species also, the margin is thin, but not scarious. On some specimens some of the larger leaves lie out at nearly 90° to the axis, and some of them are twisted in such a way as to bring the leaf surfaces parallel with the axis (Fig. 2D at top). They thus show the same sort of twisting as is seen in the larger leaves of *V. wolganensis* and is very common in the conifers, bringing the leaves apparently into two rows. On the other hand, other shoots present the leaves edge on (Fig. 2E). As in Figs. 2A, D the leaf apex may be either blunt or acute, generally more acute in the larger leaves. Fig. 2A shows an apex surrounded by a cluster of leaves, suggesting that the shoot was of unlimited growth.

The cuticle is more easily prepared, in my material, from Nattai Bulli and (especially) Oakdale than from the localities on the coast, where material is rather metamorphosed. The two sorts of cuticle are shown in Pl. 1D, indicating that except for a difference in thickness, in this species the two surfaces are extremely alike; while Fig. 5A, including a length of the margin, shows that the wrinkling found in the other species may be absent, suggesting that the leaf is flat. Where the stomata are fairly close set on the upper leaf surface the cells are scarcely in rows at all. (Pl. 1D, Fig. 5B), the arrangement of the stomata varying considerably even on the same leaf, from grouped (Fig. 5B) to scattered (Pl. 1D). Likewise the arrangement of subsidiary and encircling cells varies the commonest sort seen being the sort in Fig. 7D. The stomata themselves, on the other hand, are rather uniform and extremely like those of the other species. As in them, the cuticle is entirely devoid of papillae or sinuosities of the cell outlines, though in the more battered pieces of cuticle it sometimes looks as if the cell outlines had holes in them. This is probably sand damage.

The shoots from New South Wales are not, so far, associated with *Voltziopsis* cone units. They are referred to *Voltziopsis* because of their close resemblance to *V. wolganensis* with its cone. The type material of *V. africana* (Potonié 1899) is badly preserved, but shows a shoot with leaves about the same size as mine, and of a similar shape, though some may be more acutely pointed than is usual. In the later material (Potonié 1900), shoots are figured showing foliar dimorphism just like mine. These resemblances are held to justify identification.

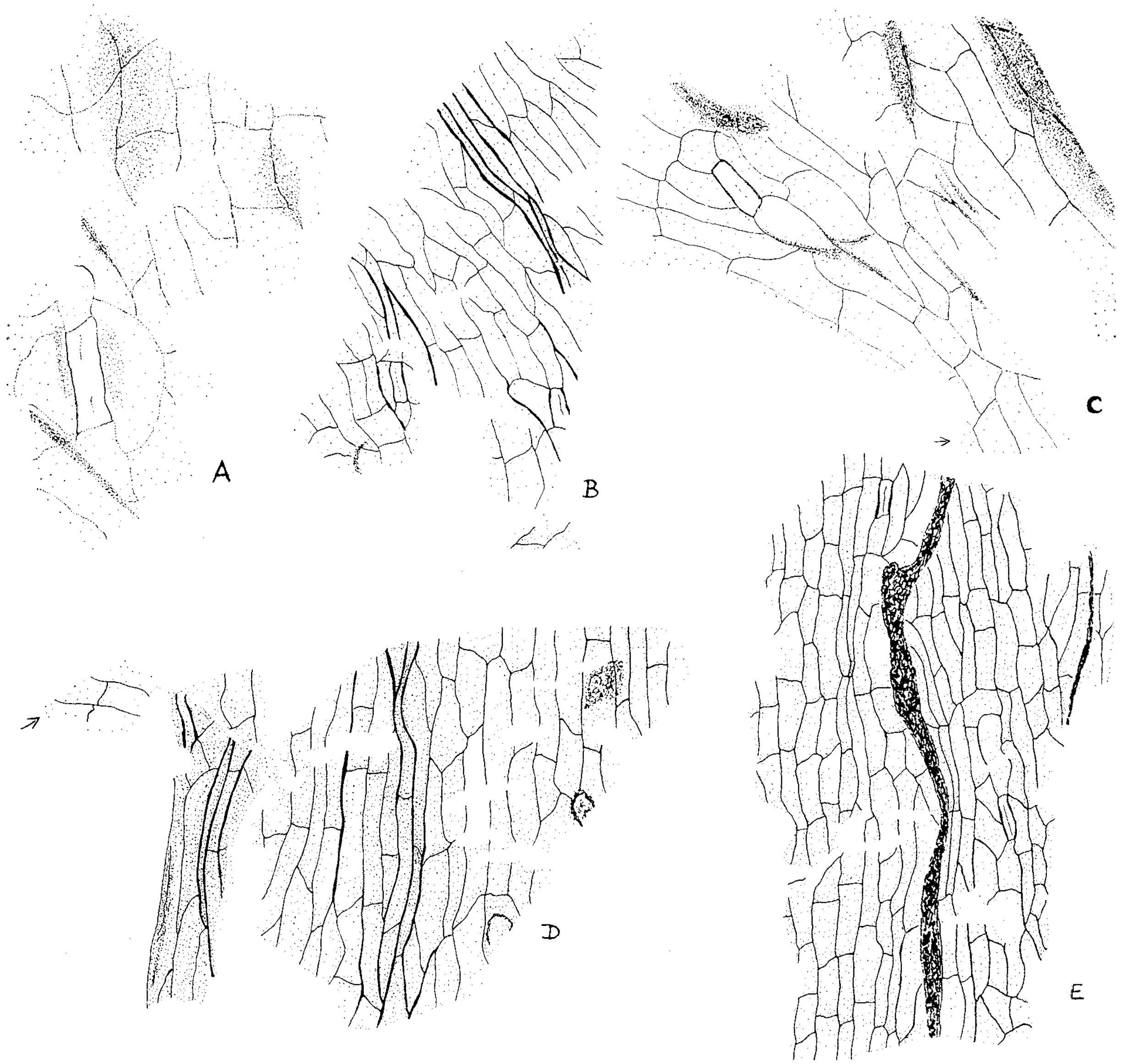

FIG. 4.—*Voltziopsis africana*, A; *V. wolganensis*, B-E. A: Fragment of cuticle with stoma x 600. B, D: Cuticle from cone scale, B upper surface joining onto D at arrow. x 200. F 2260. C: Cuticle from bract, ? of adaxial bract surface. x 200. F 2260. E: Cuticle from leaf lower surface. x 200. F 2260.

Seward (1934) and Florin (1944) confined the name *V. africana* to the cone units; it is now extended again to cover the shoots on circumstantial, but fairly impressive, evidence. First, cone units of *Voltziopsis wolganensis* are attached to shoots so similar to the isolated shoots of *V. africana* that distinguishing them is not always easy. Second, cone units and foliage are found associated in four or five localities in Africa and Madagascar (Potonié 1899, 1900; Seward 1922, 1934; Gothan 1927; Carpentier 1934, 1935), though not yet in Australia.

The diagnosis of the cone is based entirely on Florin's (1944) account, except that the seeds are considered even in this species to be inverted. Some figures of certain units (e.g. Florin 1944 Pl. 181-182, fig. 4 (lobe to right) and especially Carpentier 1935 Pl. 5 figs. 10, 11) show a line crossing the proximal parts of the lobes of the seed scale in just the way that the micropylar end of the seed in *V. wolganensis* does (Fig. 3F). Florin admitted that the point was uncertain (p. 487), and it is not now settled, though Florin's reconstruction has been copied without his hesitation (Schweitzer 1963).

Voltziopsis wolganensis sp. nov.

Pl. 1, figs. 2C; 3A, C, E, F; 4B-E; 5D, E; 6D; 7E.

1934 *Voltziopsis* Seward, pl. 20, fig. 10. Single shoot, from E. Africa.

1935 *Voltzia* cf. *heterophylla* forma *brevifolia* Carpentier, pl. 4, fig. 3, ? fig. 5, pl. 5, fig. 3 (*Voltzia* sp.) and ? fig. 2 (*Phyllotheca* sp.) shoots from Madagascar.

Holotype. F. 6620, Geological and Mining Museum, Sydney, Pl. 1, fig. E.

Locus typicus. Constance Gorge, near Newnes, New South Wales; Triassic ? Lower Triassic.

Diagnosis. Shoot system showing branches departing at 35°-45° every 15 cms. approximately; cone terminal on a short branch about 2 cms. long. Leaves of very varied sizes, when short, more or less triangular, appressed to stem, about 1 cm. long and 3 mms. wide, grading over into long leaves, 3 cms. long, 3-4 mms. wide. Leaves 2-3 mms. thick (compressed laterally). Upper leaf surface only slightly concave, and rarely raised over midline. Leaf apex more or less acute.

Cuticle on lower leaf surface showing more or less elongated rectangular cells about 41μ x 31μ, with occasional stomata, probably about 5/mms.². On upper surface cells over midline square or polygonal, about 45μ in diameter, showing irregular rows of stomata. In the rows stomata normally orientated longitudinally, and usually monocyclic, with 4-6 (mostly 4) subsidiary cells consisting of two lateral members, sometimes divided, and two terminals. In stomatal rows stomata separated by two terminal subsidiary cells, or by an encircling cell in addition; laterally 1-3 files of epidermal cells between two stomata.

Seed cone conical, about 2.5 cms. long and 1.5 cms. wide at maximum. Bract of cone unit forked in about last third of its length, as long as to be twice as long as cone scale. Five lobes of cone scale joined into stalk about 3 mms. long, each lobe about 4 mms. long, bearing single inverted seed about 2 mm. from apex. Apex of lobes acute, lobes 1.5-4 mms. wide. Cuticle on cone unit showing cells set more or less in rows, about 58μ x 30μ; stomata monocyclic or only rarely incompletely dicyclic, otherwise as on leaf. Seeds 1.5 mms. long and 1.0 mm. wide, fused seed stalk showing as a slight ridge about 0.25 mm. wide.

(i) *Description and discussion*: The material consists of a single specimen, F6620, in the Geological and Mining Museum, and I am most grateful to the Director of the Geological Survey of New South Wales and Dr. J. Pickett for allowing me to examine the specimen.

The locality is given as Constance Gorge. Unluckily two places have held this name. At present it is applied to a small gorge leading S.E. into Rocky Gorge and thence into the Wolgan River some five miles *downstream* from Newnes. Dr. Pickett and I walked through this system of gorges without finding anything the slightest bit hopeful. However, earlier, the name Constance Gorge was applied to an even smaller gorge (communicating, by one of the very few practicable passes through the sandstone walls confining the Wolgan Valley, with the present Constance Gorge) running W. into the Wolgan 2 miles *upstream* of Newnes. The sidings of the old Newnes Railway lay in this earlier named Constance Gorge and my guess is that the specimen was found during the building of the Newnes Railway, a work involving extensive excavation. The whole countryside is still only sparsely settled and very difficult. This matter is of importance, for if the specimen comes, as I suspect, from the earlier named Constance Gorge, it is definitely Lower Triassic, but if from the valley now holding the name, it may be either Lower or Middle Triassic (Hawkesbury). In this area both Narrabeen and Hawkesbury are very unfossiliferous.

There is some suggestion that small leaves alternate regularly with long ones (Pl. 1E), and just possibly this may be seasonal, for a slightly comparable variation in leaf length can be seen over a year's increment in *Podocarpus ferrugineus* Bidwill, and doubtless others. The leaves, however, are much the same shape whether long or short (Pl. 1E and Fig. 2C). Judging from the form of the compressed leaves, the upper surface was only slightly concave, and in a few places, when the leaf is compressed laterally, shows a low keel over the midline (Fig. 2C). The venation is unknown, as in all species.

The form of the cuticle is given in the diagnosis and in Figs. 4, 5 and 6. As with all species, the material breaks up into small pieces on maceration. It is not known whether there was a non stomatiferous zone over the midrib or not. In Fig. 6D to the left there appears to be an area devoid of stomata, and since the fragment comes from the central parts of the leaf this may represent a "midrib". In no stoma can one see any sign of papillae or lappetts.

The cone is attached by a short length of branch, with leaves just like any other (Pl. 1C). On the cone the bracts are strongly decurrent, but at the level of the cone scale, which emerges at about 90° from the main cone axis, turn out (Fig. 3F). It is difficult to see the bract on the cone, and its form is only clearly seen on the isolated cone unit in Fig.

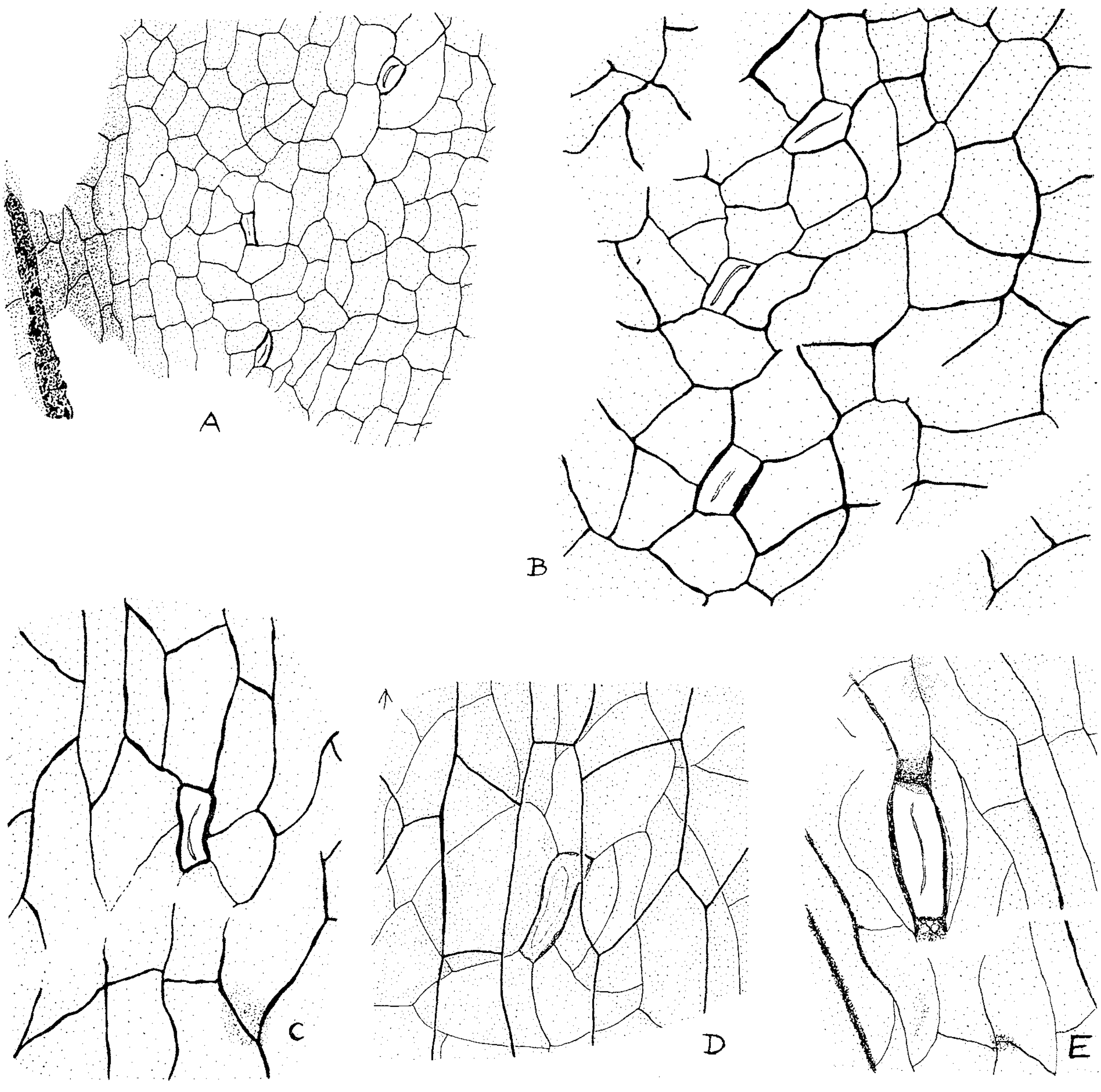

FIG. 5.—*Voltziopsis africana* A-C; *V. wolganensis* D, E. A: Cuticle towards margin of a leaf. x 200. 3001. B: Cuticle with three stomata with subsidiary cells touching. x 400. 3001. C: A stoma with rather few subsidiary cells. x 600. 3000. D: Cuticles from the cone scale, stoma present on one. x 600. F 2260. E: Stoma from leaf. x 600. F 2260.

3C, but several pieces show what is probably its forking end. Much of the same difficulty applies to the cone scales. In this material, however, only units with five lobes have been seen. The apex is most usually more or less acute (Fig. 3E), but in some it is more obtuse. The cone cuticle has already been discussed, and is shown in Figs. 4B, D.

(ii) *Note on associated pollen*. In two preparations pollen was found sticking to the cuticle of the leaf in groups, of three grains, and of two very badly preserved ones. So far as I can tell all is of the same sort.

The grains are disaccate, about 150μ in total width, with a corpus about 120μ wide and 120μ long. The grain in Fig. 3G is interpreted as a slightly rotated lateral longitudinal view, for it shows the striae towards the proximal (as interpreted) end of the grain, on both surfaces, but not at the distal. This specimen is slightly torn at the cappula, but shows that there was no colpus. The sacci are attached by heavily staining roots, and project slightly distally, and in the specimen figured are not continuous with one another (pseudo-monosaccate), but they are in another grain. The ornament consists of the usual recticulum on the sacci, perhaps with the muri somewhat radially disposed.

The corpus is round or oval in polar view, but slightly narrower at the cappula than the cappa (Fig. 3G), and its edge is taken to be marked by the strong line just inside the saccus roots. The striae are seen as very fine sometimes anastamosing grooves; twelve and ten are visible on the two best grains. In the grain figured the central stria is flanked by two rather heavy exinal thickenings, but in another grain, compressed laterally, all striae are alike (cf. the variations in the monolete mark of *Rissikia*).

There is no distinct evidence that these grains belong with *Voltziopsis*, but when one finds an extremely rare fossil associated with some rare pollen (Balme 1963) *set in groups*, the possibility is raised that the two belong together (cf. Harris 1964, pp. 176-178).

The grains are extremely like, though larger than, the grain named *Striatites sp.* cf. *Taeniaesporites antiquus* Leshik of Balme (1963, p. 26, pl. 6, fig. 13), which comes from the lowest Triassic (Kockatea Shale) in Western Australia. It also resembles the grains now named *Stroterporites richteri* Klaus and *S. jansonii* Klaus (1963), as Balme says. These grains show an especially prominent central stria, sometimes bifurcating (Klaus 1963, pl. 15); and it is believed that one of my grains showed a similar structure (above, and Fig. 3G). However, two other grains definitely do not show such a large stria. The point can be taken no further without more material. I do not think it would help to formalise these grains with a binomial and it is not clear what genus they should go into (cf. Hart 1964, pp. 1181, 1186).

(iii) *Specific comparisons*. *V. wolganensis* is distinguished from *V. africana* on three grounds. Its leaves are more dimorphic, longer and narrower than those of *V. africana*, while the stomata are mostly surrounded by only four subsidiary cells divided distinctly into lateral and terminal members, and not, as in *V. africana*, surrounded by a ring of subsidiary cells (Figs. 5B; 6D). However, there are intergrading leaves and many intergrading stomata, and I imagine that the distinction will only be really clear in good material. In addition, the lobes of the seed scale complex are more or less acute in *V. wolganensis* but obtuse in *V. africana*, though here too there are vexing intermediate cases (e.g. Carpentier 1935, pl. 5, fig. 10).

Voltziopsis augusta (Walkom) comb. nov.

Figs. 1B-D; 2F; 6A-C; 7A-C.

1922 *Ullmannia* sp. Seward, pp. 389, figs. 2-5. From Tanganyika.

1925 *Brachyphyllum angustum* Walkom, p. 221, pl. 30, figs. 5, 6.

1940 *Brachyphyllum angustum* Walkom: Florin, p. 49. Review only.

1944 *Walkomia primula* Frenguelli, pp. 300-306, pl. 5, figs. 1-5.

Holotype: Walkom 1925, pl. 30, fig. 5, the branched shoot to left.

Locus typicus: Turimetta Head, New South Wales; Gosford Formation, Upper Narrabeen Group, Lower Triassic.

Diagnosis emended. Sparingly branched shoots having short leaves about 3 mms. long (minimum) and 3-4 mms. wide, varying up to long leaves 1 cm. long, of same width. Leaf upper surface only slightly concave, but no sign of keel over "midrib" seen. Leaf 1.2 mms. thick (compressed laterally). Leaf apices more or less acute, margin thin but not scarious.

Cuticle on lower leaf surface 1.5-2μ thick, showing more or less square to slightly elongated cells, running in rows. Cells about 35μ across. No stomata seen on undoubted lower leaf surface. Cuticle on upper leaf surface at margins as on lower surface, margins about 8 cells wide. Elsewhere cells more or less square, about 40μ across, but less regularly in rows. Stomata scattered, or lying distant from one another in vague rows. Stomata with longitudinal to (more often) irregular orientation, mono, or dicyclic, subsidiary cells 4-8 (mostly 5 or 6) forming a ring and not always separable into lateral and terminal members. Surface of subsidiary cells smooth, and encircling cells quite unspecialised except by position. Stomata separated by at least 2 or 3 epidermal cells. Guard cells somewhat sunken in rounded pit, about 25μ in diameter, subsidiary cell ring sometimes slightly sunken. Guard cells feebly cutinised except round aperture. Cell outline on lower surface 3-6μ thick, on upper 2-6μ, neither showing sinuosites, processes or pitting.

Description and Discussion. The material examined consists of three short lengths of shoot on one block (F13022), and two fragments on a second (F13021). Both are unlocalised but F13022 almost certainly comes from Turimetta Head, since it is in a collection some of which was definitely localised as Turimetta by Walkom (1925); and the matrix looks indistinguishable from material I have collected at Turimetta. I have failed, however, to rediscover this conifer. F13021 is not from Turimetta, but, again judging from the matrix, may have been discovered (along with a good many

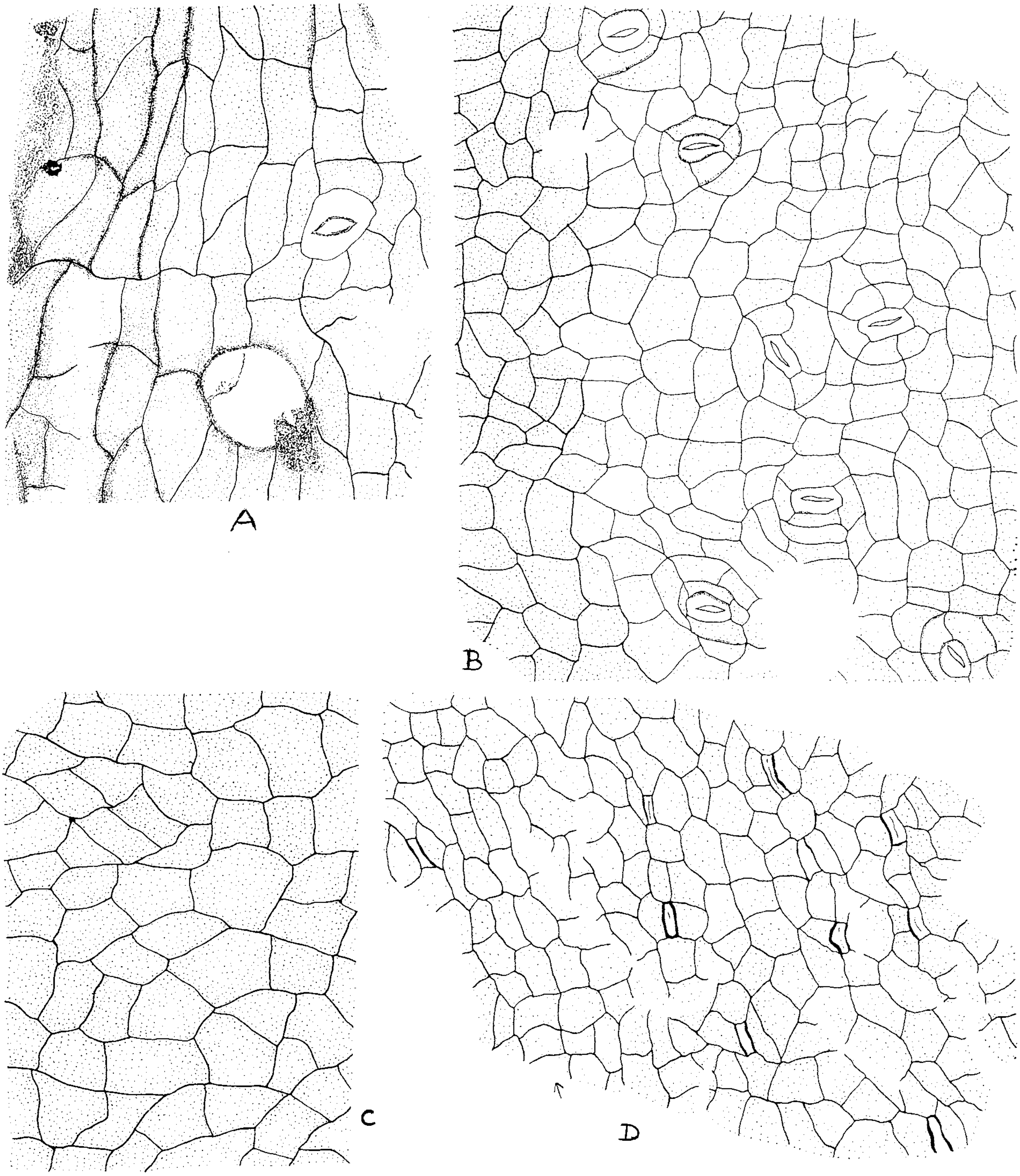

FIG. 6.—*Voltziopsis angusta*, A-C; *V. wolganensis*, D. A: thick cuticle, probably from leaf lower surface, and a stoma. x 400. F 13022. B: Cuticle from upper leaf surface, heavier stipple to left taken to mark midrib. x 400. F 13021. C: Cuticle from leaf lower surface. x 900. F 13022. D: Cuticle from leaf upper surface, arrow marking position of possible midrib. x 400. F 2260.

other fossils) when the swimming baths at Narrabeen were dug. Walkom's (*loc. cit.*) specimens are neither in the Australian Museum, nor the Geological and Mining Museum, nor in either University collection. They seem to be lost.

The leaves are shown in Figs. 1 and 2. They display the same sort of dimorphism as *V. wolganensis*, but less extremely. Even the long leaves are directed forwards, and show no sign of twisting into two ranks. Normally parts of four leaves can be seen in any place on a stem (Figs. 1B, 2F; Fig. 2F at a branch), but on some of the smaller pieces only three may be visible (Fig. 1C). The leaf shape in section is reconstructed as in *V. africana* (see above, p. 179). As in that species, the leafy margin is thin, but not scarious and shows in some cuticle preparation wrinklings of the sort seen in Fig. 4D.

In the cuticle preparations in which both surfaces could be associated, or followed through maceration, no stomata at all could be found in the thicker (presumably lower) cuticle. In one place, however, (Fig. 6A) there is a somewhat substantial cuticle, showing one stoma, and this may be from the lower leaf surface. The probability is (on the assumption already discussed as to the orientation of the cuticle fragments) that the leaf was entirely or almost entirely epistomatic. Stomata are less commonly met with in preparations from long leaves, and it is possible that, within limits, the number of stomata is fixed per leaf, but more material is needed to confirm this speculation.

The cells and cell outlines are shown in Figs. 6 and 7. The stomata are most varied. At one extreme (Fig. 6D) there are no encircling cells, and the stomatal apparatus comes close to *V. wolganensis;* at the other (Fig. 7C) the stomata is more or less reguarly dicyclic. However, in all seen the pit is rounded rather than rectangular, and the subsidiary cells do not usually fall easily into terminal and laterals. Judging both from focussing, and from differences in shade, the whole circle of encirling cells may be sunken slightly.

Except for the possible difference in stomatal density, the cuticular details of all the shoots, as well as the leaf shape in section, is the same. Thus only one species is present. It is most unfortunate that Walkom's specimens are lost especially as the description given is uninformative. Judging from dimensions, and from the figures, there are no differences between Walkom's material and mine, unless it be that Walkom's shoots are rather smaller (e.g. his Pl. 30, fig. 6), but this seems to be matched (Fig. 1C). As noted, part of my material is probably from Turrimetta, which was Walkom's locality. On these grounds, I identify my material with Walkom's.

Walkomia primula Frenguelli (1944) is another difficult case, for again the description lacks detail. It is identified because, on evidence available at present, the differences between it and the New South Wales material are slight. Dimorphism of the leaves is not mentioned, but some would seem to be present (see Frenguelli 1944, pl. 5, figs. 3, 4, 5); certain specimens may be narrower, than the normal, but they can be matched, at least to some extent (Frenguelli 1944, pl. 5, fig. 4 and Fig. 1C). The leaves of *W. primula* are narrower than usual, but so they are in Fig. 1D. Until cuticular detail is known there appears to be no grounds for maintaining *W. primula* as a separate species. However, the cuticle of Frenguelli's specimens has not been examined. The name *Walkomia* was misapplied by Florin (1944, p. 370, footnote). This is of no consequence if, as seems probable, *Walkomia primula* is identical with *Voltziopsis angusta.*

Seward's (1922) material lacks detail, but in what can be seen it agrees closely with *V. angusta,* and is therefore separated from *Ullmannia,* with which agreement is not very close, and identified with *V. angusta.*

The reason for placing *V. augusta* in *Voltziopsis* is that in its leaf shape and cuticle it comes extremely close to the two species of *Voltziopsis*

TABLE I.

Comparison of Voltziopsis species

	V. africana	*V. wolganensis*	*V. angusta*
Leaves	Up to 1 cm. long, 5 mms. wide apex obtuse; slightly twisted into 2 ranks	Up to 3 cms. long, 3-4 mms. wide, apex acute, when large twisted into two ranks	Up to 1 cm. long, 2-3 mms. wide, apex acute, never twisted into 2 ranks
Stomatal distribution	Unequally amphistomatic, stomata ± in rows	Unequally amphistomatic, stomata ± in rows	Almost or quite epistomatic, stomata set irregularly
Subsidiary and encircling cells	Stomata mostly monocyclic, rarely incompletely dicyclic subsidiary cells often forming ring of 4-6, but not sunken	Stomata mainly monocyclic, subsidiary cells mostly four, and not sunken	Stomata mostly incompletely dicyclic, subsidiary cells set in a ring, often slightly sunken
Cone scale	Lobes obtuse, bract not much longer than cone scale	Lobes acute, bract (when seen) notably longer than cone scale	NO INFORMATION

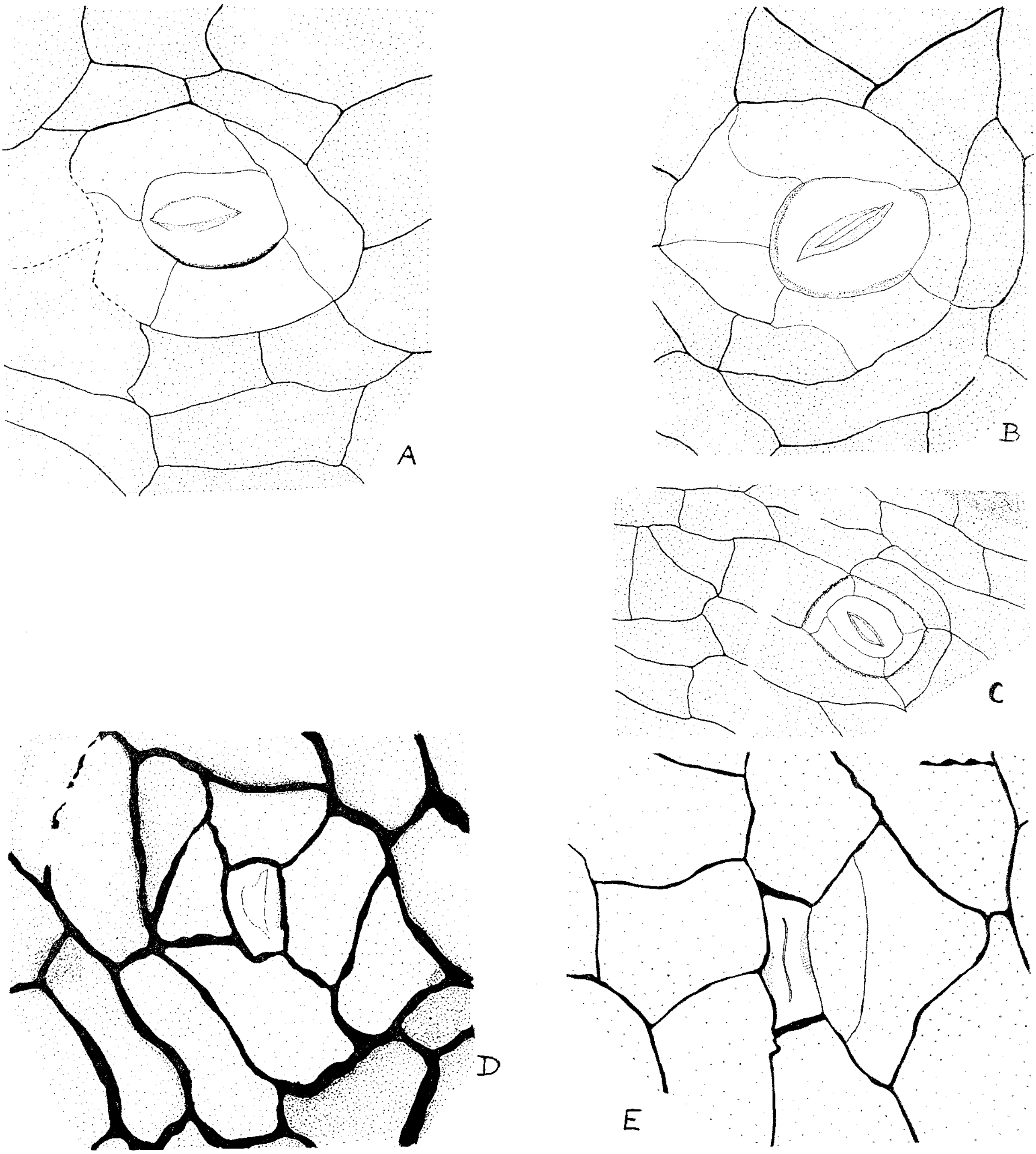

FIG. 7.—*Voltziopsis angusta*, A-C; *V. africana*, D; *V. wolganensis*, E. A-C: Stomata, A from a long leaf, partly dicyclic, B from a short leaf, C from a short leaf, monocyclic. A, B x 600, C x 400. F 13022. D: A stoma, partly dicyclic, with subsidiary and encircling cells tending to form a ring (cf. Fig. 5A.) x 600. 3001. E: A stoma of the sort most often seen, and with one subsidiary cell divided. x 600. F 2260.

known with cones. It is slightly younger than either of the others, but occurs in the same region, and in a similar flora. The situation is therefore just like that in which leaves of, say, *Athrotaxis* from the Australian early Tertiary are ascribed to a living genus, and the evidence somewhat stronger than that for ascribing Tertiary conifer shoots to *Metasequoia* when they come from regions where *Metasequoia* is not now found. A further reason is that Seward (1922) found seed cone units rather like *Voltziopsis* with his material.

The three species of *Voltziopsis* may be compared as below (Table I).

GENERAL DISCUSSION

As here interpreted *Voltziopsis* is a genus of conifers, having shoots all of one sort, dimorphic leaves, triangular or crescentic in section, with a thin cuticle with somewhat scattered, not regularly alligned simple stomata mostly or (possibly) all on the upper surface of the leaf; with compact seed cones, having forked bracts and five-partite (rarely six-partite) cone scales, each lobe being adnate to the stalk of one inverted seed. These conifers are probably Lower Triassic. The chief lack is any knowledge of the pollen cone, though it is possible that the pollen corresponds broadly with *Stroter-sporites* Wilson (Klaus 1963).

With this information they seem to diverge sharply from nearly all other Upper Permian and Lower Triassic conifers, including the podocarpaceous *Rissikia*. The (isolated) cone most closely comparable is *Swedenborgia* Nathorst (see Harris 1935), which has essentially the same construction (including the long stalk to the cone scale), differing only in the bract, which is small and adnate to the cone scale in *Swedenborgia* but free and forked in *Voltziopsis*. However, reduction in size and adnation of the bract to the cone scale is a general feature of conifer evolution, and I doubt whether this difference between *Voltziopsis* and *Swedenborgia* is of much significance. The foliage of *Swedenborgia* is not known, but Harris (1935) suggested that it might belong to *Podozamites*: if so, this would be a most important difference between the two conifers. It is of interest that the stomata of *Swedenborgia* resemble those of *Voltziopsis*, though their structure is so generalised that little weight can attach to this resemblance. Florin (1944) points out that *Swedenborgia* has essentially the same structure as the *Cryptomeria* seed cone, and could therefore stand close to the *Taxodiaceae*. The same argument may be applied to *Voltziopsis*, and some other facts are consistent with it. The leaf form of *V. wolganensis* and *V. angusta* is rather like that of *Athrotaxis selaginoides*, as is also the stomatal distribution. The arrangement of subsidiary cells recalls *Cryptomeria* (see Florin 1931) but not the stomatal arrangement which in *Cryptomeria* is in zones. The way in which the stomata of *V. africana* may lie in groups with their subsidiary cells touching recalls *Athrotaxis*, especially *A. laxifolia* Hook. though here the subsidiary cells may be shared, and in *A. selaginoides* there is only a single large group or mass of stomata covering most of the upper leaf surface. The irregular orientation of the stomata is seen in the Taxodiaceae, but in other places as well, e.g. *Araucaria*, where the subsidiary cell arrangement is different. If the associated pollen should prove to belong to *Voltziopsis*, this is an important matter, though not one that rules out a connection with the Taxodiaceae (cf. *Pinus* L. and *Larix* Mill.) The leaf dimorphism of *Voltziopsis* finds some but not a complete parallel in species of *Taxodium* Rich. and *Glyptostrobus* Endl. (Florin 1931 pls. 6 and 7.)

I do not place *Voltziopsis* in the Taxodiaceae, believing that unless we have foliage and both sorts of cones agreeing with, or explicable in terms of, a living family, such an ascription is premature. We have as yet no right to assume that the Triassic conifers all belonged to the families now living, though they may ultimately prove to do so (cf. *Cherolepidium* (Schimp.) Takhtaj.). The Family Voltziaceae (Pilger and Melchior 1954), an assembly of diverse fossils, provides a convenient resting place for the moment.

Schweitzer (1963) has carefully re-examined *Pseudovoltzia* Florin, and while confirming Florin at most points, shows that this genus generally has two seeds only per cone scale, not three. He proceeds to argue that the majority of conifers can be derived from *Pseudovoltzia*. In the sense that very many conifer cones can, by what Bower once called a morphological *tour de force* be derived from *Pseudovoltzia*, this is true. In the sense that any phylogenetic connection is likely, I reject the argument for *Voltziopsis* as for *Rissikia*. Evolution in the conifers at large, and in the Podocarpaceae and Taxodiaceae has in general tended to reduce the number of parts, and orders of branching. Scheitzer's view implies first an increase in number of seeds, then a decrease. This is complicated and unnecessary. Beside, there are considerable other differences between the cones, and so much as is known of the foliage of *Pseudovoltzia, Rissikia,* and *Voltziopsis*. *Pseudovoltzia* is Upper Permian in age, the others definitely date from the Lower, and probably basal, Triassic, and on palynological evidence may be even older, as old in fact as *Pseudovoltzia*. This, to my mind, does not give time for the complex evolution necessary.

Equally I can see no very obvious connections between *Voltziopsis*, (and *Rissikia*, see the first of these notes) and *Lebachia* Florin. Doubtless both derive ultimately from that complex of very early conifers of which *Lebachia* was a rather specialised member; but that would seem to be the whole extent of any connection.

The southern conifers, *Rissikia* and *Voltziopsis* suggest another view of conifer evolution, with which indeed, the known facts about the northern Triassic and later Permian conifers are consistent, though this view remains speculation.

Supposing that the conifer flower was originally radially organised, evolution proceeded, as Florin has shown, towards flattening and reduction of parts. In the podocarpaceae a trimerous symmetry seems to have resulted; in the Pinaceae (with which *Glyptolepis* Schimp. and *Pseudovoltzia* compare) we have only two "megasporophylls" but several sterile lobes; it is possible that in the Taxodiaceae, with which de Laubunfels (1965) would associate the Cupressaceae, as in *Voltziopsis* and *Swedenborgia*, five lobes each associated with a seed is basic, other patterns occurring (e.g. *Cunninghamia* R. Br. with three lobes to the seed scale complex); while in the Araucariaceae, perhaps a single lobe and "megasporophyll" is basic, as it is in *Ullmannia* Goepp., though the cone scale details are different. There is at least some evidence for tracing each of the supposed lines of evolution into the Permian, and I suggest the possibility that each arose independently of the others, perhaps as early as the Carboniferous. This suggestion is far from original.

If the pollen associated with *V. wolganensis* does really derive from it, we have an interesting situation paralleling what is found in *Rissikia*. The pollen is known first from the Northern Hemisphere Permian, but, as far as is known, only from the base of the Triassic in Gondwanan areas (Balme 1963). This suggests, as Balme showed, that part of the early Triassic Gondwanan flora was immigrant from northern lands, these conifers perhaps being in that immigrant part.

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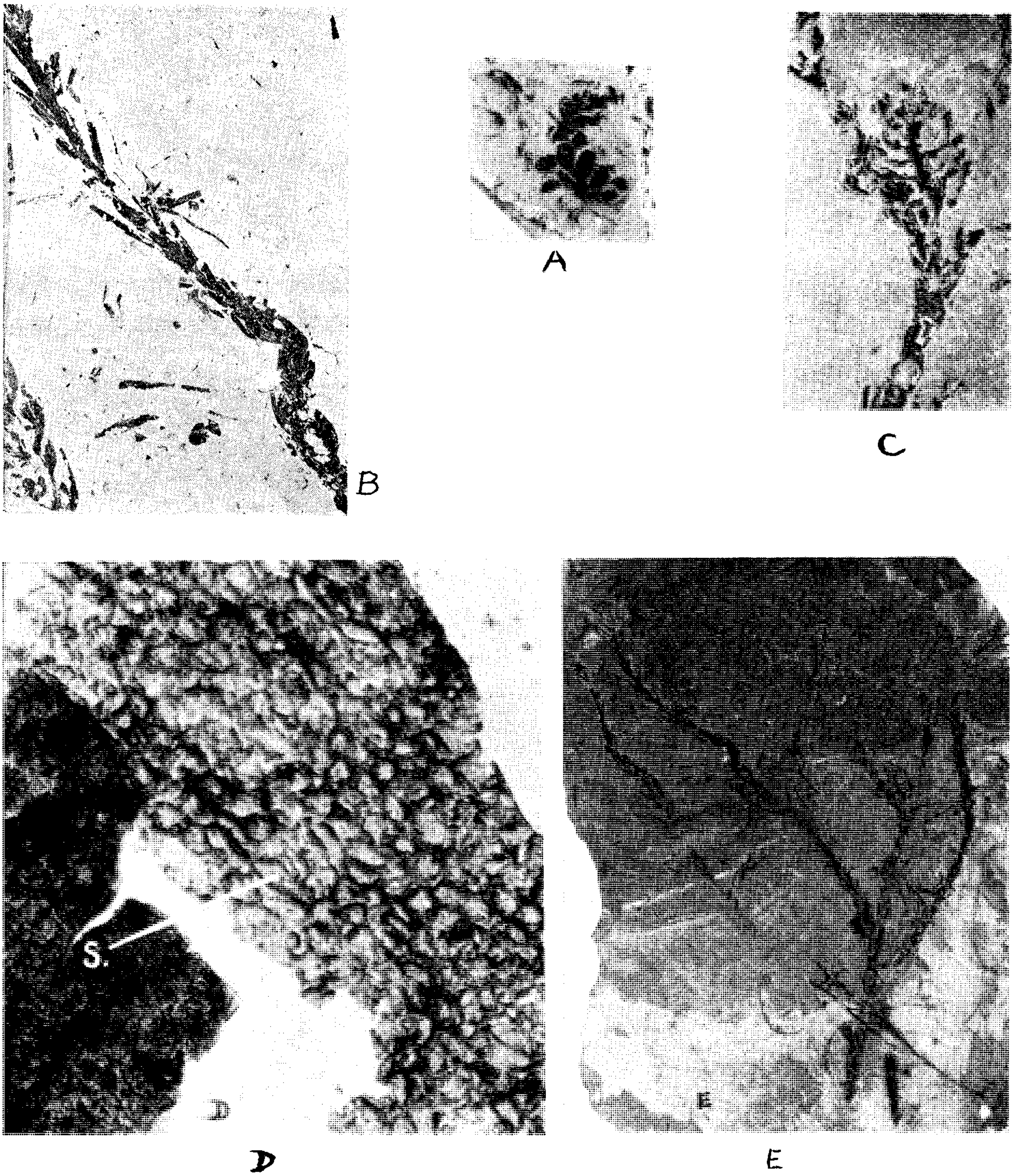

PLATE I.—*Voltziopis africana* A, D: *V. wolganensis*, B, C, E. A: short length of shoot, x 1; 2968; B: Part of a shoot showing different leaf sizes, x 1; C: The seed cone attached to its branch, x 0.75; D: Cuticle from two leaf surfaces (upper to right), a stoma at *s* x 100, 3001: E: The whole specimen x 0.3. B, C, E, F 6620.